

THE EFFECT OF SUBMERGENCE ON SEED GERMINATION IN TREES FROM AMAZONIAN FLOODPLAINS

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ABSTRACT – Rapid and exactly timed seed germination is essential for the establishment and survival of seedlings in Central Amazonian floodplains, where the non-flooded period is short. The peak of fruiting occurs at high water, and the seeds must tolerate extended periods of flooding and often submergence. Germination starts immediately after the retreat of the flood, but it is not clear if submergence is directly responsible for the inhibition of seed germination. In the present paper, an experiment was performed with twelve tree species from Amazonian floodplains to test whether seed germination occurs only in non-flooded seeds. Ten pairs of each species consisting of 1 plastic cup + seed + soil, and 1 cup + seed + soil + water (5 cm) were tested for germination. Thirty to 100 % of the non-submerged seeds germinated after seven weeks. Four species showed radicle growth, but no species produced a shoot as long as it was submerged. Independent from phylogenetic constraints and from growth strategies among the twelve chosen species, the timing of germination was closely linked to retreating flood water, guaranteeing efficient seedling establishment in the floodplains prior to re-submergence.

KEY WORDS: Amazonian floodplains, Seed germination, Submergence, Tree establishment, Viability.

ABSTRACT – O período exato e rápido da germinação de sementes é essencial para o estabelecimento e a sobrevivência de plântulas em áreas alagáveis da Amazônia Central, onde a fase terrestre é limitada. O pico de frutificação ocorre durante a fase aquática, e as sementes

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têm que suportar extensos períodos de inundação e, muitas vezes, de submersão. A germinação inicia-se imediatamente com a fase terrestre mas, por enquanto, não está claro se a submersão é diretamente responsável pela inibição da germinação. Neste trabalho, realizou-se um experimento com 12 espécies das áreas alagáveis da Amazônia para testar se a germinação ocorre somente em sementes não-inundadas. Em dez pares de cada espécie consistem em 1 copo plástico + semente + solo, e 1 copo plástico + semente + solo + água (5 cm) foi testada a germinação. Entre 30% e 100% das sementes não-inundadas germinaram após 7 semanas. Quatro espécies mostraram crescimento de raiz, mas nenhuma espécie produziu um caule durante o tempo de inundação. Independente da constituição filogenética e das estratégias de crescimento das doze espécies selecionadas, a velocidade de germinação está relacionada ao decréscimo da inundação, garantindo um estabelecimento eficiente nas áreas alagáveis.

PALAVRAS-CHAVE: Áreas inundáveis, Germinação, Submersão, Estabelecimento, Viabilidade, Amazônia.

INTRODUCTION

Plant establishment in Central Amazonian floodplains occurs in the terrestrial rather than aquatic period. On the lower levels in the flooding gradient, the non-flooded phase may be as short as 5 months. Rapid and exactly timed seed germination is, therefore, essential for the establishment and survival of the seedlings. The peak of fruiting in most species occurs at high water, several weeks to months before dry land appears after the receding flood (Worbes 1997; Wittmann & Parolin 1999), in order to guarantee dispersal by water and fish (Goulding 1983). Therefore, the seeds must tolerate extended periods of submergence. Kubitzki & Ziburski (1994) observed that there is a fine-tuned mechanism of dormancy that enables the diaspores to start germinating immediately after the retreat of the flood. Nevertheless, it is not clear whether submergence is directly responsible for the inhibition of seed germination. The present experiment aimed at answering the question: does seed germination of Amazonian floodplain trees occur only under non-flooded conditions?

MATERIAL AND METHODS

Twelve tree species from Central Amazonian floodplains were chosen for this study. They display a wide variety of ecological features including distribution (occurrence in nutrient-rich whitewater floodplains or nutrient-poor blackwater floodplains), successional status (pioneer/non-pioneer), leaf phenology (evergreen/deciduous), level in the flooding gradient, and germination type (epigeal/hypogeal) (Table 1).

Mature seeds of each species were collected during the period of high water levels (July/August) in the floodplains of the Rio Amazonas (Solimões) and Rio Negro in the vicinity of Manaus, Brazil. They were transported to the Amazon Research Institute (INPA) in Manaus and kept in plastic basins filled with river water, which was changed at 3-d intervals until the experiment started. All species were subjected to submergence for 6-33 d before the experiment. This was necessary because not all seeds matured at the same time, and because some species (e.g. *Crateva benthami*, *Tabebuia barbata*, *Nectandra amazonum*) require submergence to break dormancy (Ziburski 1991). Seeds of all species, intended for other experiments, were kept in the water-filled basins for up to 76 days.

The germination experiment was performed at an open experimental site at the INPA below a tree, so that it was sunny in the morning and in the afternoon, but shady between 11.00 and 14.00 h. Air temperature varied between 23°C and 35°C, with an average of 30.8°C during the experimental period. Soil and water temperature did not exceed 30.1°C, with an average of 28.9°C. The timing of the experiment corresponded to the non-flooded period, in which seedling establishment occurs naturally in the field.

Ten pairs of seeds of each species, consisting of 1 plastic cup (300 ml) with 1 seed and well watered floodplain soil or 1 cup with 1 seed, floodplain soil and floodplain water, were tested for germination. Seeds were sown on the soil surface and submerged

Table 1. Twelve species chosen for this study, with different distribution (seeds collected in nutrient-rich whitewater floodplains W, in nutrient-poor blackwater floodplains B), successional stage (P pioneer, NP non-pioneer, *sensu* Swaine and Whitmore 1988), leaf phenology (E evergreen, D deciduous), level on the flooding gradient (L low: 18-25 m asl, H high: 25-28 m asl), diaspores sink (S) or float (F), and germination type (E epigeal, H hypogeal); in order by family.

Family	Species	Seed collection site	Successional stage	Leaf phenology	Level in flooding gradient	Diaspore sinks / floats	Germination type
Caesalpinaceae	<i>Aldina latifolia</i> Spruce ex Benth.	B	NP	E?	H	F	H
	<i>Campsandra comosa</i> Benth.	B	NP	E	L	F	H
	<i>Cratdia amazonica</i> Spruce ex Benth.	B	NP	D	L	F/S	H
	<i>Mora paraensis</i> Ducke	B	NP	D	H	F	H
	<i>Senna reticulata</i> (Willd.) Irwin & Barn	W	P	E	H	S	E
Fabaceae	<i>Swartzia polyphylla</i> DC.	B	NP	D	H	F	H
	<i>Vatairea guianensis</i> Aubl.	B	NP	D	H	F	H
Bignoniaceae	<i>Tabebuia barbata</i> (E.Mey.) Sandwith	W	NP	D	L	S	H
Capparidaceae	<i>Cratogeomys benthianii</i> Eichler	W	NP	D	L	S	E
Cecropiaceae	<i>Cecropia latiloba</i> Miq.	W	P	E	L	F/S	E
Lauraceae	<i>Nectandra amazonum</i> Nees	W	NP	E	L	S	H
Verbenaceae	<i>Vitex cynosa</i> Benth.	W	NP	D	L	F	E

by a water column of approximately 5 cm. Evaporated water was replaced daily. Germination was calculated as the number of seeds that germinated after 7 weeks in relation to the total initial seed number (in percent). The form of germination was differentiated as seed swelling (after absorption of water), radicle growth, and shoot growth.

A statistical analysis (ANOVA) of the differences in germination defined as number of radicle emergence between non-submerged and submerged seeds was performed with SYSTAT.

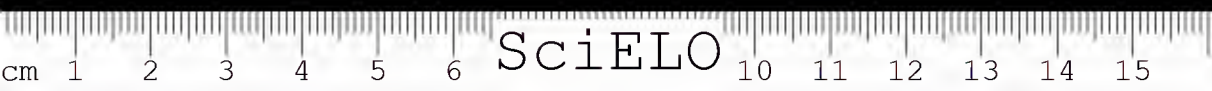
RESULTS

In the unsubmerged conditions, 30 to 100 % of the seeds of all species germinated (at least radicle emergence) after seven weeks (Figure 1). Of the submerged seeds, seven species opened after swelling (10 - 100% of the planted seeds), but in five they remained unchanged. Only four submerged species showed radicle emergence, and no seeds of any species exhibited germination of the shoot (Figure 1). The statistical analysis showed highly significant differences in germination, defined as radicle emergence, between non-submerged and submerged seeds in nine species ($P < 0.05$) (Table 2).

Seeds were flooded between 6 and 33 days in the plastic basins prior to initiation of the experiment. The seeds of *Crudia amazonica* and *Tabebuia barbata* were viable at least for a month, but most of the seeds of these two species started to rot thereafter. In the other ten species, seeds remained visually sound at least for 63-76 days (data not shown).

DISCUSSION

The present experiment showed that seed germination of Amazonian floodplain trees occurs mainly in non-flooded seeds. Submerged seeds of some species may initiate germination, which is shown by the emergence of a radicle, but no species was able to produce a shoot as long as it was submerged. The seeds of the floodplain trees



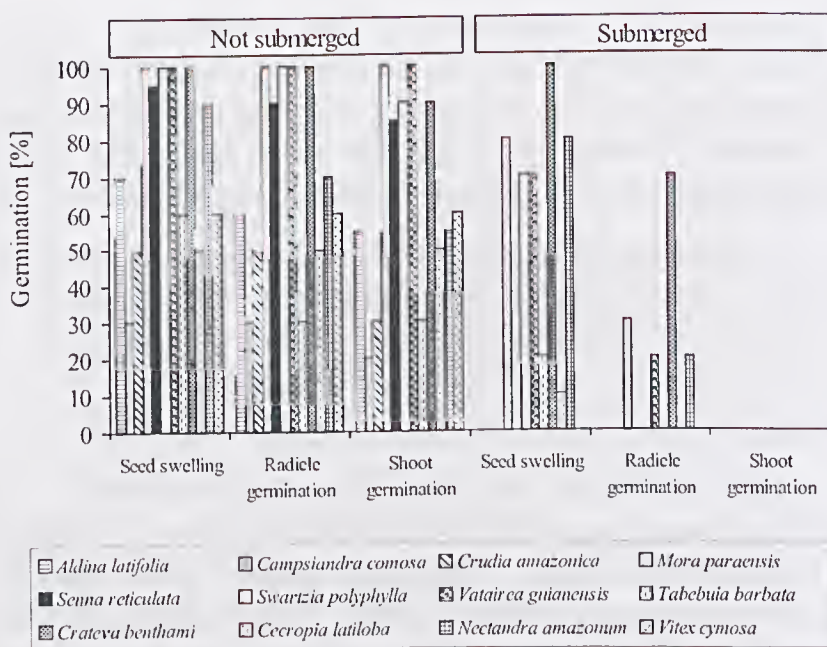


Figure 1 - Seed germination (seed swelling, emergence of the radicle or the shoot) in twelve species from the Central Amazonian floodplains in seeds placed on a wet soil surface under submerged or unsubmerged conditions.

are very well adapted to the changing environment. After fruit maturation, the seeds fall into the water and may be submerged for several weeks. Whether they float or sink (Table 1), they do not germinate until the flood recedes and the conditions are favourable for seedling growth. Competitive advantages can be achieved by germination under water if the flood regime is shallow and short lived. Under deep and prolonged flooding, as in central Amazonian floodplains, the capacity of seeds to remain dormant or quiescent under water tends to prevent losses of entire seed crops. Also, seeds of the species that dominate the swamps in the southern United States (*Taxodium distichum*, *Nyssa aquatica*, *Nyssa sylvatica*) do not germinate under water, and the natural regeneration is usually limited to drought periods when the soil surface is exposed (Hook 1984). A number of bottomland hardwood species may germinate under water, but the

Table 2. Results of statistical analysis (ANOVA) of the differences of germination defined as radicle emergence between non-submerged and submerged seeds of the twelve study species ($P > 0.05$).

	F-ratio	P
<i>Aldina latifolia</i>	13.500	0.002
<i>Campsandra comosa</i>	3.857	0.065
<i>Cecropia latiloba</i>	9.000	0.008
<i>Crateva benthami</i>	3.857	0.065
<i>Crudia amazonica</i>	9.000	0.008
<i>Mora paraensis</i>	21.000	0.0001
<i>Nectandra amazonum</i>	6.081	0.024
<i>Senna reticulata</i>	81.000	0.0001
<i>Swartzia polyphylla</i>	100	0.0001
<i>Tabebuia barbata</i>	3.857	0.065
<i>Vatairea guianensis</i>	36.000	0.0001
<i>Vitex cymosa</i>	13.500	0.002

flooding regime on such sites is usually shorter and shallower than in Amazonian floodplains. Hence, germination under water may have some ecological significance (DuBarry 1963).

As long as the seeds of the chosen species were in the water, they remained viable. Seeds which were kept in the air dried or decomposed within a few days (e.g. *Tabebuia barbata*, *Nectandra amazonum*) or weeks (e.g. *Senna reticulata*, *Aldina latifolia*), whereas submerged seeds of ten of the 12 species remained viable for at least 60 days if the water was changed frequently (Parolin 2001). This stands in contrast to the majority of land plants, whose seeds lose their viability if submerged for prolonged periods (Hook 1984). Seeds that opened under water had a higher viability than seeds that remained closed: a higher percentage germinated, and they germinated faster after water receded, compared with the non-swollen seeds of all species.

Although seed mass (Parolin 2000) and establishment strategies (Parolin 1998) vary considerably among the chosen species, the patterns of germination were rather similar between them, even when phylogenetic relationships are considered, e.g. within the Caesalpiniaceae to which 5 of the 12 chosen species belong. Independent from phylogenetic constraints, a close relationship between retreating floodwater and germination has evolved which guarantees proper timing for efficient seedling establishment in the floodplains prior to re-submergence.

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